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THE LAST PREMEIOTIC MITOSIS AND ITS RELATION TO MEIOSIS IN GAILLARDIA[1]

By Sanford Atwood

Department of Botany, University of Wisconsin

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In a recent review of chromosome structure, Kaufmann[2] concludes the majority of work favors the interpretation that somatic anaphase and telophase chromosomes contain two more or less intertwined chromonemata and that somatic metaphase chromosomes are four-parted. He mentions the last premeiotic mitosis but concludes that further investigations of pre-leptonema stages are necessary for critical analysis of the late meiotic prophases. Several recent investigators report that the time of splitting of the chromonemata is the same in the last premeiotic as in any other somatic mitosis, but none could discriminate the last premeiotic division absolutely from other archesporial divisions. The difficulty is due in large part to the spore mother cells often being very numerous and irregularly arranged in plants selected for their large chromosomes. Huskins[3] and his co-workers, developing the "Unified Theory," have admitted the duality of anaphase chromosomes in every mitosis except the last premeiotic division. Darlington,[4] on the other hand, has denied the duality of all mitotic anaphase chromosomes, as a fundamental premise for his "Precocity Theory."

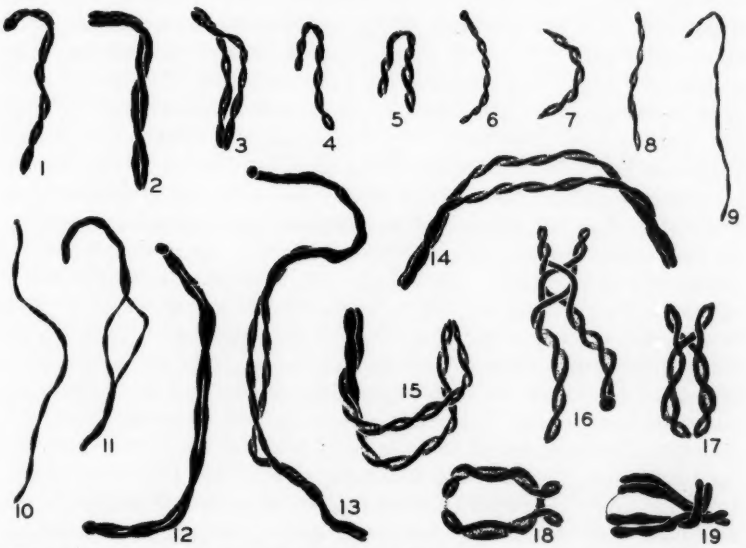
The plants used in this investigation belong to four cultivated varieties of *Gaillardia aristata*. The gametophytic chromosome number is 36 in all four varieties. Cooper and Mahony[5] have previously reported a count of $n = 18$ for one race of this species. The double number of chromosomes and the occasional presence of quadrivalents at meiosis indicate that the cultivated varieties used in the present study are probably autotetraploids. These forms were selected for two reasons. First, the nearly flat head bears many flowers which are at only slightly different stages of development. In longitudinal sections of such heads, the anther sacs show progressively older stages tracing from the centermost to the outside flowers. In large heads with 10 to 12 flowers in cross-section, the difference in development between adjacent flowers is so slight that

all stages from the last premeiotic division to the heterotypic equatorial plate can be seen in a single section. Second, the sporogenous tissue in the anther sacs is constantly four-rowed and almost invariably 30 to 35 cells in length. This regular arrangement of spore mother cells is maintained at least through pachynema. If a delayed somatic mitosis is found among a row of 30 or more resting sporogenous cells, it may be concluded with reasonable certainty that the two nuclei resulting from this division are not themselves likely to divide before meiosis.

Figures 1 to 9 show stages in the last premeiotic mitosis, determined as just described. At late prophase (Fig. 1) the two halves of each chromosome are twisted about each other; all the evidence indicates that these twists have remained intact from the preceding telophases. In an early equatorial-plate stage (Fig. 2) the number of twists is considerably reduced. Somewhat later (Fig. 3) the two halves are completely unwound, and each half or daughter chromosome is now seen to contain two chromonemata spiraled in the same direction and about each other. The exact time of the division of each daughter chromosome into two chromonemata was not determined; it may occur during the prophases, but in these medium-sized chromosomes it is not optically demonstrable until a late equatorial-plate stage. During the anaphases (Figs. 4, 5) the two chromonemata in each daughter chromosome still coil in the same direction and about each other. Occasionally the direction of coiling is reversed in the two arms of a single chromosome. In case the stain is so dark as to obscure the separateness of the chromonemata, the whole chromosome has a wavy appearance, wide and narrow regions alternating along its length. These wide and narrow regions are interpreted as places at which the two chromonemata in the course of their coiling lie respectively side by side or one above the other. After the anaphasic massing at the poles the twists may be somewhat tightened (Fig. 6), but by middle telophase (Fig. 7) the two chromonemata within each chromosome again are very distinct. At late telophase stages (Fig. 8) the chromosomes seem to elongate, the two chromonemata thus being brought closer together. As the resting stage is approached (Fig. 9) the chromonemata are even more closely approximated. On this interpretation each darkly staining continuous thread in the resting nucleus represents two chromonemata closely appressed rather than a single chromonema that has separated from its sister. Despite the close approximation of the chromonemata, a wavy outline is still apparent for each chromosome as a whole, resulting according to the present interpretation from the intimate coiling about each other of the two sister chromonemata of each chromosome. Because a large number of divisions such as described above have been observed and found to show the same chromonematal relations as are found in other mitoses in anther sacs and root tips, it is concluded that the last

premeiotic division in *Gaillardia* is similar in all respects to any other mitosis.

During leptonema the two sister chromonemata of each chromosome are not easily demonstrable, but any thread that can be traced for a considerable distance through a nucleus still shows a distinctly wavy outline (Fig. 10). Since the threads are now even more extended than were



Figures 1–9. Semi-diagrammatic drawings of the last premeiotic mitosis. Figure 1. Prophase. Figure 2. Early equatorial plate. Figure 3. Late equatorial plate. Figure 4. Early anaphase. Figure 5. Late anaphase. Figure 6. Early telophase. Figure 7. Middle telophase. Figure 8. Late telophase. Figure 9. Resting stage. Figures 10–19. Semi-diagrammatic drawings of the meiotic prophase. Figure 10. Leptonema. Figure 11. Zygonema. Figure 12. Pachynema. Figure 13. Early diplonema. Figure 14. Late diplonema. Figure 15. Early diakinesis. Figures 16–18. Middle diakinesis. Figure 19. Late diakinesis. All figures drawn at table level with an Abbé camera lucida, using Zeiss 2 mm. apochromatic objective, N. A. 1.40, and Spencer compensating ocular 30×; magnification c. 4300×.

those observed during the relatively short premeiotic resting period, it seems probable that the two sister chromonemata of each chromosome are now even more closely appressed. At zygonema stages in which the homologous chromosomes have not yet paired completely (Fig. 11), each chromosome still displays a wavy outline. In certain pachynema figures in which the separate chromosomes of a pair are distinguishable, each homologous chromosome likewise has a wavy outline (Fig. 12). From

leptonema through pachynema a distinct "bouquet" is evident in most spore mother cells. The regular orientation of threads, the majority spraying out from one side of the nucleus, is considered to be directly related to their regular orientation in the anaphases and telophases of the last premeiotic division. A synizetic knot is not conspicuous at any time, although the "bouquet" arrangement involves a certain degree of unilateral grouping. As the chromosomes shorten and thicken in diplonema stages, the two chromonemata within each member of a pair are again apparent (Figs. 13, 14). If such a stage is darkly stained, the wavy outline at least is conspicuous. At early diakinesis the two chromonemata within each chromosome are even more evident (Fig. 15), still coiled about each other in the same direction just as they were in the anaphases and telophases of the last premeiotic division. If a chromosome pair is oriented favorably at middle diakinesis, chiasmata are often observable (Figs. 16, 17). The two chromonemata of each chromosome are now quite distinct and appear to be farther apart than at earlier stages, but they are still coiled about each other in the same direction within each member of the pair. In general, the spirals within a single chromosome run in the same direction on both sides of a chiasma. Because of this relationship and because of the fact that the two chromonemata of a chromosome seem to remain twisted about each other continuously from the last premeiotic anaphases and telophases, it is concluded that opening out in the pair could have occurred only on the reductional plane. This line of evidence for the one-plane theory of chiasma-formation might be added to those recently summarized by Sax.[6] The chiasmata were undoubtedly formed at some earlier stage when pairing was more intimate. Some evidence for them was obtained at diplonema stages, but most chiasmata are not clearly demonstrable until diakinesis. The coils of the chromonemata appear in some cases to run in the same direction in both members of a chromosome pair (Fig. 16); in other cases they run in opposite directions (Fig. 17). In a few cases reversals of twist occur (Fig. 18). Bivalents observed during later stages of diakinesis show that the chiasmata gradually move toward the ends of the chromosomes. With the coiled relationships involved here, this process of terminalization necessarily results in some untwisting of the chromonemata. At very late diakinesis terminalization, together with an untwisting of the remaining coils, eventually results in the separate chromonemata or chromatids of each member of a pair coming to lie almost parallel (Fig. 19). Each chromatid now presents a somewhat wavy outline which may indicate its doubleness. At the heterotypic equatorial plate the straightening is completed, and at heterotypic anaphases, as in many other plants, the two chromatids of each univalent may diverge widely except at the point of spindle-fibre attachment.

Summary.—In four tetraploid ($n = 36$) varieties of cultivated *Gaillardia aristata* the last premeiotic mitosis is shown to be similar to any other mitosis, each anaphase and telophase chromosome containing two chromonemata spiraled in the same direction and about each other. The last division before meiosis is located by finding delayed somatic mitoses in sporogenous tissue of an anther sac which is constantly four-rowed and almost invariably 30 to 35 cells in length. By tracing the chromonemata from the prophases of the last premeiotic mitosis to the heterotypic metaphases it is concluded that each thread in the premeiotic resting nucleus represents two chromonemata closely appressed and that the coiling relationships of the last premeiotic division persist through to the heterotypic prophases. Evidence was obtained from the direction of the chromonematal coils near chiasmata that chiasmata must be formed according to the one-plane theory.

[1] The writer wishes to express sincere gratitude to Dr. C. E. Allen for suggesting the problem and for constant advice and criticism throughout the cytological study and the writing of the manuscript.

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AN EVOLUTIONARY ANALYSIS OF INSULAR AND CONTINENTAL SPECIES

BY ALFRED C. KINSEY

DEPARTMENT OF ZOÖLOGY, INDIANA UNIVERSITY[1]

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Discussions of evolutionary problems usually fail to take into account the varying constitution and behavior of species among different groups of plants and animals. The species problem becomes a number of problems if there are a number of different entities that pass as species. Quite aside from confusions introduced by differing concepts and definitions of the basic taxonomic unit, the qualities of inter-breeding populations among such diverse things as, for instance, strong-flying birds, parasitic insects, world-circling primates, microscopic fungi, bacteria, slow-fruiting angiosperms, and crustacea of the ocean plankton are so various that no single, simple explanation, or any theoretic ideal, can account for the evolution of all of them.

The relatively few forms which have been subjected by the geneticists to laboratory studies do not reflect the diversity which exists in nature; and

any extensive application of the laboratory data on evolution must await exhaustive taxonomic analyses of a variety of organisms. Until then evolutionary theorists can hardly know what conditions the theories must cover. In studies on the gall wasp family Cynipidae I have attempted to make such an application of the laboratory genetics. Experimental breeding is hardly possible with these insects because of their relatively long life cycles, peculiar life histories which involve an alternation of generations, and strict relations to particular plant hosts; but these very qualities are the sources of unusually significant material for taxonomic analyses of certain evolutionary phenomena.

On the immediate question of insular and continental species I can summarize data from the study of nearly 400 species of gall wasps belonging to the genera *Neuroterus*, *Cynips*, *Disholcaspis*, *Xystoteras* and some other smaller groups. The 75,000 miles of field work have been spread throughout the United States, Mexico and Guatemala in order that the analyses might cover all of the available species of the complexes and genera involved.

The opportunity to analyze insular species among these insects depends on the fact that each gall wasp is restricted to a single kind of oak or to a limited number of related oaks as hosts. Among the more than 300,000 individuals handled to date only 10 (i.e., 0.003%) have occurred on anything else than their normal hosts. Further isolation is also provided by the limitation of the oak hosts throughout most of the western United States, Mexico and Central America to high mountain elevations which stand like so many oceanic islands in a sea of deserts and tropic lowlands. For many groups of plants and animals the desert mountain ranges of our Southwest and Mexico offer better opportunities for the study of isolation than that afforded by any group of oceanic islands.

Practically all of the Cynipidae studied to date are classifiable as insular or continental forms. Only a few of the wider ranging species occurring in continuous mountain areas are not classifiable as one or the other of these types. Some 76% of the gall wasps studied are insular. Similar analyses of some other groups for which there are adequate taxonomic data show 74% insular species among the salamanders of the family Plethodontidae (Dunn 1926), 62% among the cave crickets of the genus Ceuthophilus (Hubbell 1936), possibly 15% among the pondweeds of the genus Potamogeton (Fernald 1932) and only 9% among the spiderworts of the genus Tradescantia (Anderson and Woodson 1935). Outside of oceanic island forms, there are few insular species among most groups of birds or mammals. Thus the number of insular forms varies widely in different groups, and the Cynipidae undoubtedly represent an extreme case but one that is matched among other forms more often than is usually recognized.

Most of the insular Cynipidae are located in the western half of the United States, Mexico and Central America; all of the continental species are found in the eastern half of this country and in Europe. In the western American and Mexican mountain areas the diversities of the topography directly effect the isolation of the insects, and indirectly limit them by isolating the species of oaks on which they occur. The only insular species in the eastern half of the United States and in Europe are those that are isolated by their hosts; but the oak species usually range so widely in these areas that most of the Cynipidae on them are continental in nature.

The ranges of the insular species are on a whole very much smaller than those of continental forms. The record is as follows:

	Ranges in Square Miles		
	MINIMUM	MAXIMUM	AVERAGE
225 Insular species	100	50,000	4,600
64 Continental species	10,000	1,500,000	300,000

For a third of the insular species the ranges are 500 miles or less in extent; half of them have ranges which cover less than 2000 square miles. Half of the continental forms have ranges of more than 200,000 square miles. Since the size of a range has some relation to, even if it is not an exact parallel of, the number of individuals involved it may be said that continental species usually represent a hundred times as many individuals as insular species. The largest continental species may involve 15,000 times as many individuals as the smallest insular species. These great differences in the sizes of specific populations are the primary bases of the differences in their evolutionary histories.

The individual variation found in these insects has been recorded in other publications.[6-9] If, in summary, we put the species in five groups according to the extent of variation within each, we have the following data:

	SPECIES STUDIED	VERY CONSTANT	FAIRLY CONSTANT	VARIABLE	HIGHLY VARIABLE	MOST EXTREME
Insular Species	158	82%	12%	4%	..	2%
Continental Species	39	..	13%	74%	13%	...

Four-fifths of the insular species are more constant than any of the continental species; four-fifths of the continental species are distinctly variable; and yet the three most extreme instances of intra-specific variation occur among what are distinctly insular species from the mountains of Colorado and Utah. The uniformity usually found among the insular forms appears to depend upon the smaller sizes of the populations involved. Other factors being uniform, there is less chance that major mutations will appear in small populations. Again, as Wright has emphasized (1931),

near homogeneity should be reached more quickly in a small, freely interbreeding population than in a large, partially subdivided group. To a large extent the hypothesis is verified by the facts; but as with all considerations of chance, the analyses of specific cases show that the unexpected may sometimes happen, resulting in this case in intra-specific variation among a few of these island forms which equals or surpasses that found in continental Cynipidae.

In 94% of the continental cases, intergrading populations were found to occur between related species. Intergrades were found in only 12% of the insular species. It is to be recalled that Darwin and his contemporaries were peculiarly ignorant of the existence of inter-specific intergrades. Recently, however, the more thorough taxonomic studies are so often in accord in finding intergrades that the opinion is now current that this is characteristic of all species. The studies on which this opinion is based are, however, largely concerned with continental forms, and the cynipid data show how much continental and insular species may differ in this regard.

The interpretation of these intergrading series between species is crucial for the understanding of evolutionary processes. In the Darwinian theory, and to most taxonomists today, they represent the transitional stages in an accumulative variation by means of which the one species has evolved from the other in the series. But the absence of intergrades between insular forms indicates the need for some better explanation of their occurrence in continental areas. As I have elsewhere shown,[8,9] the differentiation of these insular species of gall wasps often involves such startling changes as the nearly complete loss of wings, the doubling or tripling in length of abdominal spines, the reduction of the whole thorax even to a half of its former size, the change from leaf to stem oviposition, striking changes in gall characters and changes in the choice of host. The differences between the most closely related Cynipidae are sometimes of such magnitude that they would rate as generic in most taxonomic practice. With such distinct characters and so many species involved, it seems improbable that intergradent types could ever have existed without leaving more evidence than we find among the insular forms today. Mutation and not accumulative variation seems to have been responsible for most of the evolution among insular groups.

Similarly it may be believed that the continental species of these same phylogenetic lines, differentiated as they are on essentially the same bases as their insular relatives, evolved in the first place as the result of mutation. But in these continental areas the opportunity for inter-specific hybridization has led to the development of large hybrid populations which lie between the original species. As I have shown in the two publications on Cynips,[8,9] the characters of these intergrading populations are precisely

what would be expected from crosses of the parental types when multiple factors are involved. Other workers find hybrid populations among other plants and animals which are located in the same portion of the United States from which we have these hybrid Cynipidae. And the final confirmation of this analysis comes from the experimental extraction of the parental stocks or synthetic production of the wild type hybrids by Anderson for species of iris,[11,12] Anderson and Woodson for several species of Tradescantia,[5] Mrs. Erlanson for roses,[13] Sumner for mice.[14,15]

In only 9 cases do the gall wasp hybrids constitute such large populations, with such uniform ranges and means of variation that they fit our definition of species as *populations having access to common stocks of genes.* The experimentalists are, however, inclined to believe that hybridization is a prime source of new types in evolution. It is again to be noted that this conclusion has been drawn from studies made in the eastern half of the continent, or from free-moving forms which are continental in nature even in the desert and mountain areas of the western portion of North America. The data do not justify the conclusion that hybridization is of great importance among insular species.

Local differences in remote portions of specific populations are characteristic of continental but rarely found in insular species.

	SPECIES STUDIED	LOCAL RACES
Insular	158	5 = 3.2%
Continental	48	17 = 35.4%

It may be expected that more adequate material will show local races occurring in many more Cynipidae than the 22 recorded above; but the distribution of the cases which we do have seems significant. There is some current opinion that local races are to be found in nearly all species. The taxonomic and genetic studies (Anderson and Woodson 1935, Dobzhansky 1933, Sumner 1934, Wright 1932) are, however, based on forms that are largely continental and not representative of that large portion of the fauna and flora which is insular in nature. The rarity of local races among insular species is clearly another consequence of the small numbers of individuals involved. In small ranges there are few physical barriers to the free and rapid interchange of genes. In the wider-spreading continental species ecologic diversities, numerous physical barriers and (probably most important of all) distance may serve as partial barriers to the ready spread of the new characters which develop in locally segregated portions of the range.

The partial isolation of portions of continental populations leads to the current conclusion that the multiplication of species is most often achieved through a subdivision of the parental range. I have tried to analyze the gall wasp material on this point; but from the field data it is

not always easy to recognize whether it is subdivision of the old range or migration of the new type to a previously unoccupied area that has accomplished the speciation. The clearest case would be one in which the derived species was more or less surrounded by the older species. Among all the Cynipidae studied, there is not a single case of this sort. Another source of evidence, however, would lie in those species which split the range of the most closely related species. The species with the discontinuous ranges may be interpreted as parental species. There are only 3 such instances among the studied Cynipidae. They all occur in continental areas, in the eastern half of the United States. Beyond these cases, it is quite possible that some of the isolated species in the insular areas represent diverse developments in what was originally a single population ranging over the several islands now occupied by the set of species. I have not discovered a good method for recognizing such a history on the basis of the field data.

On the other hand, there is some reason for believing that most of these insular species have originated on the periphery instead of in the heart of the parental range, or, more often, have moved out of the parental range into territory previously uninhabited by that specific stock. In making the phylogenetic maps for the genus *Cynips*, it has often been possible to recognize which are the older and which the derived species. In almost every instance in insular areas the younger species occupies territory (either geographic or host) removed and even remote from the areas previously occupied by the older stocks. It is notable that in his thorough analysis of the cave cricket genus *Ceuthophilus*, Hubbell (1936) reaches the same conclusion as to the development of new species on the periphery of the older ranges. On the other hand, in continental areas the phylogenetic chains in *Cynips* turn in every direction, with little geographic trend, and it is possible that in such areas subdivision of the parental ranges is a more common source of the multiplication of species.

In summary, it may be remarked that it is unfortunate that continental species have been the best known among both European and American biologists. The conditions which have made it possible for certain forms to become continental have made it inevitable that students should first of all have explored Central Europe and the eastern third of the North American continent; the very factors which have isolated insular species have removed them from the attention of the laboratory investigator. Current concepts of species as highly variable, locally sub-divided, widely intergrading populations are based upon and quite justified by the data on continental species. But among these the significance of mutation is largely concealed, and the significance of hybridization as a factor in evolution is greatly over-emphasized. Insular species, which are in actuality very common among many groups of plants and animals, are

usually quite homogeneous in constitution, show little tendency for subdivision into local populations and give rise to few inter-specific hybrids. They indicate that mutation and the early isolation of the new types are important means of increase in the number of species. In any event, insular species are simpler to interpret, and an understanding of such forms may be basic to an understanding of continental species.

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ON THE INTEGRATION OF OPERATORS

BY GARRETT BIRKHOFF

HARVARD UNIVERSITY

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Suppose one is given a system of ordinary differential equations having the special form

$$dx_i/dt = \sum_{h=1}^{r} \rho_h(t) \cdot X_i^h(x_1, \cdots, x_n) \quad [i = 1, \cdots, n]. \tag{1}$$

We propose the question: how can one find a vector-field Z such that if $x(t)$ is any solution of (1), if $y(t)$ is any solution of

$$dy_i/dt = Z_i(y_1, \cdots, y_n) \tag{2}$$

and if $x_i(0) = y_i(0)$ for $i = 1, \ldots, n$, then $x_i(1) = y_i(1)$ for $i = 1, \ldots, n$?

If one regards the vector-fields $X^1, \ldots, X^r$ as infinitesimal transformations in the sense of Lie, one sees that this question is a special instance of the following more general problem.

Let $X(t) = \sum_{h=1}^{r} \rho_h(t) \cdot X^h$ be any variable linear combination of several fixed (not necessarily linear or commutative) operators X^h operating over a specified period of time—say the interval [0, 1]. What single fixed operator Z, operating constantly over the same period, will produce the same net effect?

Under many conditions which will be stated below, Z is the sum of a formal series

$$Z = \gamma_1 Z + \gamma_2 Z_2 + \gamma_3 Z_3 + \ldots \tag{3}$$

whose terms are products $\gamma_i Z_i$ of the Poisson brackets Z_i in the X^h of different lengths* $w(Z_i)$, by scalars γ_i. Moreover each γ_i can be computed from the $\rho_h(t)$, by first finding their first derivatives $\rho_h'(t)$, and then performing at most $w(Z_i)$ multiplications and quadratures.

It follows that if the $\rho_h(t)$ are polynomials in t and $e^{\lambda_\kappa t}$—such polynomials can always be written as sums of monomials $c_j x^{n_j} e^{\lambda_j t}$—then the γ_i can be computed by rational operations on the numbers c_j, n_j, λ_j followed by reading off from a table of exponentials. For instance, this can be done in the especially interesting case that the $\rho_h(t)$ are simply periodic functions (the λ_j are imaginary).

In the commutative case, ignoring terms whose coefficients γ_i vanish, (3) assumes the trivial form

$$Z = \rho_1(1) \cdot X^1 + \ldots + \rho_r(1) \cdot X^r \tag{4}$$

and Z is simply the (linear) *average* of the $X(t)$.

If $r = 2$, then the coefficient of $Z_3 = [X^1, X^2]$ is essentially the area integral $\int (\rho_1 \rho_2' - \rho_2 \rho_1') dt$. The coefficients of the terms of higher order give one a wholly new series of interesting affine covariant path-integrals, of similar polynomials in the ρ_h and ρ_h'.

If $r = 2$, setting $\rho_1(t) = 1$ and $\rho_2(t) = 0$ on [0,1], and setting $\rho_1(t) = 0$ and $\rho_2(t) = 1$ on [1,2], the series (3) gives (locally) the function of composition of any Lie group under canonical parameters.

The series (3) gives a Z with the required properties in three important cases.

The first is the case that the X^h (together with their commutators) generate a finite continuous group—as is always the case if they are linear. In this case (3) yields a solution provided the X^h are near enough the null operator.

The second is the case that the X^h are analytical operators expressible in the form

$$X_i^h(x_1, \ldots, x_n) = \sum_j c_{ij}^h x_j + \sum_{j\kappa} c_{ij\kappa}^h x_j x_\kappa + \ldots \tag{5}$$

that is, leaving the origin fixed. In this case a similar restriction applies.

The third is the case that the X^h are linear operators on any Banach space, and have a small enough "modulus" (in the sense of Banach).

In all three cases, the restrictions on the X^h depend on the $\rho_h(t)$, and can be removed entirely provided the X^h generate a group G, the wth term of whose "lower central series"† tends to zero as $w \longrightarrow \infty$.

The proofs of the above statements will be published elsewhere.

* The "length" of a Poisson bracket is simply the number of (equal or distinct) letters in it. Thus $[[X, Y], X]$ is of "length" three; X is of "length" one.

† By the wth term of the lower central series, is meant the invariant subgroup generated by brackets of lengths $\geqq w$.

GROUPS WHICH CONTAIN AN ABELIAN SUBGROUP OF PRIME INDEX

BY G. A. MILLER

DEPARTMENT OF MATHEMATICS, UNIVERSITY OF ILLINOIS

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When a group G contains a subgroup of index 2 this subgroup is invariant under G but when it contains a subgroup of index p, p being an odd prime number, this subgroup H is not necessarily invariant under G. We shall first prove that when H is abelian and non-invariant under G then G contains an invariant subgroup of order p and also an invariant subgroup whose order is divisible by p and involves no other prime factor except factors of $p - 1$. To prove the former of these facts it should be noted that the p conjugates of H under G are transformed by G either according to the metocyclic group of order $p(p - 1)$ or according to an invariant subgroup thereof for the following reasons: If two such conjugates have a common operator this appears in the central of G since it is transformed into itself by the operators of each of these two conjugate subgroups and therefore also by an operator of order p. An operator of G can therefore not transform one of these p conjugates into itself unless it is contained therein.

As these p conjugates are transformed under G according to a transitive group of degree p and of class $p - 1$ they must be transformed thereunder either according to the metacyclic group of order $p(p - 1)$ or according to a transition subgroup thereof. Hence G is isomorphic with such a group with respect to a subgroup contained in its central. Let s be an operator of lowest order among those whose orders are powers of p and which correspond to an operator of order p in the given quotient group. The number of the operators whose order is the same as that of s and which

correspond to the same operator of order p in this quotient group is a power of p since the subgroup of G which corresponds to the subgroup of order p in this quotient group is abelian and hence contains only one Sylow subgroup whose order is a power of p.

From the preceding paragraph it results that a power of p cyclic subgroups whose common order is some power of p correspond to the subgroup of order p in the given quotient group. Hence at least one of these cyclic subgroups is invariant under G. Its order cannot exceed p since the quotient group of G with respect to the subgroup of G corresponding to the subgroup of order p in the given quotient group has an order which divides $p - 1$ and cannot be the identity since G is assumed to be non-abelian. If the order of this quotient group is $p(p - 1)/k$ then k divides $p - 1$ and an operator of lowest order in G which corresponds to an operator of order $(p - 1)/k$ in this quotient group has an order which involves no prime factors except divisors of $p - 1$. This operator and the given invariant subgroup of order p generate an invariant subgroup under G which involves p non-invariant cyclic subgroups. It is invariant because it involves operators from each co-set with respect to the central. If this invariant subgroup is not G itself then G is the direct product of it and some other subgroup.

This proves the following theorem: *If a group involves a non-invariant abelian subgroup of prime index* p *and is not the direct product of such a group and an abelian group, then this abelian subgroup is cyclic and its order involves no prime factor except divisors of* p $-$ 1. *Moreover, such a group always contains an invariant subgroup of order* p *and is solvable.* In particular, when $p - 1$ is a power of 2 the given non-invariant cyclic subgroups are of order 2^m. They are also always of this order when the transitive group according to which they are transformed is dihedral. It is always possible to construct G by establishing a p, l isomorphism between an invariant subgroup of the metacyclic group of order $p(p - 1)$, or between this group itself and an abelian group. This abelian group can usually be selected in many ways when its order is given.

When a group contains a non-invariant subgroup of prime index p then it results from the preceding arguments that it is also isomorphic to an invariant subgroup of the metacyclic group of order $p(p - 1)$ or to this group itself with respect to an invariant subgroup since the operators which are common to two such conjugate subgroups constitute an invariant subgroup of G. This subgroup is, however, not in the central of G as is illustrated when G is the dicyclic group of order $8p$. In this case the p conjugate subgroups of index p are not cyclic but quaternion. In general, when an operator s of G transforms more than one of these p conjugate Hamiltonian groups into itself the subgroup generated by s is invariant under G and its operators are transformed either into themselves

or into their inverses under G. Hence the p conjugate Hamiltonian groups are transformed under G according to the dihedral group of order $2p$ and G involves no operator of order 8 but it contains an invariant subgroup of order p for the same reason as when the p conjugate subgroups are abelian. When G contains a non-invariant dicyclic subgroup of index p it contains also an invariant subgroup besides the identity but when it contains the alternating group of degree $p - 1$ as a non-invariant subgroup of index p it is simple because it is simply isomorphic with the alternating group of degree p.

When H is non-invariant under G it is always one of two permutable proper subgroups of G. One of these can be so selected that its order is a power of p. From the fact that H is non-invariant it results that the order of G is not a power of p. A Sylow subgroup of H whose order is a power of p is of index p under a Sylow subgroup of G. The latter Sylow subgroup and H can therefore be selected as the two permutable proper subgroups of G whose product is equal to G. Each of the co-sets of G with respect to H clearly involves operators whose orders are powers of p since the first $p - 1$ powers of such an operator appear in the $p - 1$ distinct co-sets with respect to H.

Hence there results the following theorem: *If a group contains a non-invariant subgroup of prime index it is the product of two permutable proper subgroups such that one of these subgroups is a Sylow subgroup of the group.*

It was noted above that when G contains a non-invariant abelian subgroup of index p, where $p - 1$ is a power of 2, and is not the direct product of such a group and an abelian group, then there is one and only one such group in which the operators of order p are transformed under G into 2^β different powers, where 2^β is an arbitrary divisor of $p - 1$. The order of this group is 2^α, where α is an arbitrary natural number provided it is at least as large as β. In particular, there is one and only one such group of order $p \cdot 2^\alpha$ in which the operators of order p are transformed either into themselves or into their inverses, where α is an arbitrary natural number. When $p - 1$ is divisible by more than one prime number there is again only one group of a given possible order in which the operators of order p are transformed in a given manner, and when this transformation is fixed the order of this group may be increased by an arbitrary factor involving only prime numbers which divide $p - 1$. The smallest order is p times the order of the transformation of the subgroup of order p but there is no upper limit of the possible orders.

When G contains an invariant abelian subgroup of index p it does not necessarily involve an invariant subgroup of order p. In the case when this invariant subgroup is cyclic it is easy to determine the possible non-abelian groups since the group of isomorphisms of a cyclic group whose order is a power of an odd prime number is known to be cyclic and hence

it cannot involve more than one subgroup of order p. In fact, it involves one such subgroup when and only when this odd prime is either congruent to unity modulo p or is a power of p which exceeds the first power. Moreover, the order of the group of isomorphisms of a cyclic group whose order is a power of 2 is itself a power of 2. When the invariant abelian subgroup of index p is non-cyclic the determination of all the possible groups involves the determination of the sets of conjugate operators of order p in the group of isomorphisms of this abelian group and this is a problem which has not yet been solved in general. It is simplified by the fact that the group of isomorphisms of an abelian group is the direct product of the groups of isomorphisms of its Sylow subgroups.

Aside from the trivial case when a group is the identity it is always generated by a smaller number of operators than its order contains units. In fact, the smallest number of operators in a set of independent generators of a group cannot exceed the index of the largest power of 2 which does not exceed the order of the group, since two operators in a set of independent generators of a group generate a group whose order is at least 4 while three such operators generate a group whose order is at least 8, etc. The abelian group of order 2^m and of type 1^m obviously contains m independent generators whenever $m > 0$. Hence the given limit cannot be reduced in the general case. A group whose order does not exceed 1000 can therefore not have as many as ten independent generators.

ALGEBRAIC THEORY OF CONTINUOUS GEOMETRIES

BY J. v. NEUMANN

INSTITUTE FOR ADVANCED STUDY, PRINCETON N. J.

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Introduction. 1. This note continues the analysis of the geometrical systems $L = L_n$, $n = 1, 2, \ldots$ ($(n-1)$-dimensional projective or *discrete geometries*) and $L = L_\infty$ (*continuous geometries*), introduced in two preceding notes of the author.[1] The axioms I–VI characterizing these systems were given in the first note (C. G.), where the properties of the unique *numerical dimension function* $D(a)$ ($a \epsilon L$) were also discussed. The second note (E. C. G.) contained examples of L_∞ establishing at the same time certain connections of systems L_∞ with abstract algebra, while other, more general, connections of this kind were mentioned. In this note we shall go considerably further: A complete characterization of our systems L in terms of algebraic ring-theory will be described.[2]

Again only results and outlines of proofs will be given, the details being reserved for a subsequent publication.

Coördinates and Ideal Theory. 2. A discrete (projective) geometry L_n is related to algebra by the possibility of describing it in terms of coordinates. This "coördinatization" of L_n is usually described as follows: Let $\mathfrak{d}$ be a not-necessarily-commutative but associative division-algebra; by a *left-ratio* we mean n elements of $\mathfrak{d}$, $\xi_1, \ldots, \xi_n$, not $\xi_1 = \ldots = \xi_n = 0$, combined to a symbol $[\xi_1 : \ldots : \xi_n]$ with the understanding that $[\xi_1 : \ldots : \xi_n] = [\eta_1 : \ldots : \eta_n]$ if and only if an element $\tau \neq 0$ of $\mathfrak{d}$ with $\tau\xi_1 = \eta_1, \ldots, \tau\xi_n = \eta_n$ exists. The left-ratios form the $(n-1)$-dimensional projective space $P_{n-1}[\mathfrak{d}]$. A set $\mathfrak{A}$ of n-uplets $(\xi_1, \ldots, \xi_n)$ from $\mathfrak{d}$ is a left-ratio-set (hence a subset of $P_{n-1}[\mathfrak{d}]$), if α) $(\xi_1, \ldots, \xi_n) \epsilon \mathfrak{A}$ implies $(\tau\xi_1, \ldots, \tau\xi_n) \epsilon \mathfrak{A}$. If furthermore β) $(\xi_1, \ldots, \xi_n), (\eta_1, \ldots, \eta_n) \epsilon \mathfrak{A}$ imply $(\xi_1 + \eta_1, \ldots, \xi_n + \eta_n) \epsilon \mathfrak{A}$, then $\mathfrak{A}$ is a *linear subspace* of $P_{n-1}[\mathfrak{d}]$. These $\mathfrak{A}$ form a system $L_n[\mathfrak{d}]$ which is a partially ordered set, if $\mathfrak{A} \subset \mathfrak{B}$ means set-theoretical inclusion, and a lattice by (a) $\mathfrak{A} \cap \mathfrak{B} = gr.l.b.(\mathfrak{A}, \mathfrak{B})$ = set-theoretical intersection of $\mathfrak{A}, \mathfrak{B}$; (b) $\mathfrak{A} \cup \mathfrak{B} = l.u.b.(\mathfrak{A}, \mathfrak{B})$ = set of all $(\xi_1 + \eta_1, \ldots, \xi_n + \eta_n)$, where $(\xi_1, \ldots, \xi_n) \epsilon \mathfrak{A}$, $(\eta_1, \ldots, \eta_n) \epsilon \mathfrak{B}$. A "coördinatization" of L_n has been achieved if the lattices L_n and $L_n[\mathfrak{d}]$ are isomorphic—$\mathfrak{d}$ being the *coördinate-division-algebra* of L_n.

The "points" of L_n, that is the minimum elements $\neq$ zero, the elements of dimension $\frac{1}{n}$ (cf. C. G., p. 100, footnote 13), correspond to those $\mathfrak{A}$ of $L_n[\mathfrak{d}]$ which consist of exactly one left-ratio—that is to the left-ratios themselves.

One of the most important facts in projective geometry is that every L_n with $n \geqq 4$ [3] is lattice-isomorphic to one and (up to isomorphic changes of $\mathfrak{d}$) only one $L_n[\mathfrak{d}]$. $\mathfrak{d}$ is obtained by v. Staudt's famous "algebra of throws," cf. V.-Y.,[4] p. 157, which establishes the (up-to-an-isomorphism-) uniqueness of $\mathfrak{d}$ also. The "coördinatization" (isomorphism of L_n and $L_n[\mathfrak{d}]$) is then achieved by routine methods, cf. V.-Y.,[4] pp. 190–200 for $n = 4$ (3 dimensions).

3. An attempt to carry this procedure over from discrete (projective) geometries L_n to the continuous ones L_∞ is *prima facie* blocked by the rôle of *points* in "coördinatization": The left-ratios $[\xi_1 : \ldots : \xi_n]$ are in a one-to-one correspondence with the points of L_n, and there are no points at all in L_∞! We shall, however, find an equivalent formulation which is not open to these objections.

Let $\mathfrak{d}_n$ be the *ring* of all nth order matrices $X = (x_{ij})$, $i,j = 1, \ldots, n$, all $x_{ij} \epsilon \mathfrak{d}$ with the usual definitions

$$(x_{ij}) + (y_{ij}) = (x_{ij} + y_{ij}), \quad (x_{ij})(y_{ij}) = \left(\sum_{k=1}^{n} x_{ik} y_{kj}\right).$$

Let us determine all *left-ideals* $\mathfrak{a}$ in $\mathfrak{d}_n$, that is all those sets $\mathfrak{a}$ for which A) $X \epsilon \mathfrak{a}$ implies $ZX \epsilon \mathfrak{a}$ for all $Z \epsilon \mathfrak{d}_n$, B) $X, Y \epsilon \mathfrak{a}$ imply $X + Y \epsilon \mathfrak{a}$. We proceed in several steps.

(i) Let $\mathfrak{a}$ be a left-ideal. Assume $X = (x_{ij}) \epsilon \mathfrak{a}$. Put $Z = (\epsilon_{ij})$, $\epsilon_{ij} = 1$ for $i = \kappa$, $j = \lambda$, but $= 0$ otherwise. Then $ZX = (x'_{ij}) \epsilon \mathfrak{a}$, where $x'_{\kappa j} = x_{\lambda j}$, but $x'_{ij} = 0$ for $i \neq \kappa$.

(ii) Let $\mathfrak{A}$ be the set of all n-uplets $(x_{11}, \ldots, x_{1n})$ for all $(x_{ij}) \epsilon \mathfrak{a}$ (that is: of all first rows in the $X \epsilon \mathfrak{a}$). Put $Z = (\tau \delta_{ij})$ ($\delta_{ij} = 1$ for $i = j$, but $= 0$ otherwise), then our A) for $\mathfrak{a}$ implies α) in 2 for $\mathfrak{A}$. B) for $\mathfrak{a}$ implies β) in 2 for $\mathfrak{A}$. Hence $\mathfrak{A}$ is a linear subspace of $P_{n-1}[\mathfrak{b}]$.

(iii) If $(x_{ij}) \epsilon \mathfrak{a}$ then every n-uplet $(x_{i1}, \ldots, x_{in}) \epsilon \mathfrak{A}$: Put $\kappa = 1$, $\lambda = i$ in (i).

(iv) Assume that n n-uplets $(x_{i1}, \ldots, x_{in}) \epsilon \mathfrak{A}$ ($i = 1, \ldots, n$) are given. So $(x_{ij}^{(h)}) \epsilon \mathfrak{a}$, $x_{1j}^{(h)} = x_{hj}$. By (i) with $\kappa = i$, $\lambda = 1$ then $(y_{ij}^{(h)}) \epsilon \mathfrak{a}$, where $y_{hj}^{(h)} = x_{hj}$, but $y_{ij}^{(h)} = 0$ for $i \neq h$. So $(x_{ij}) = (\sum_{h=1}^{n} y_{ij}^{(h)}) = \sum_{h=1}^{n} (y_{ij}^{(h)}) \epsilon \mathfrak{a}$.

(v) Combining (iii), (iv): $\mathfrak{a}$ is the set of all those (x_{ij}), for which every n-uplet $(x_{i1}, \ldots, x_{in})$ ($i = 1, \ldots, n$) is $\epsilon \mathfrak{A}$.

(vi) By (ii), (v) $\mathfrak{a}$ and $\mathfrak{A}$ determine each other uniquely. One verifies immediately that if a linear subspace $\mathfrak{A}$ of $P_{n-1}[\mathfrak{b}]$ is given, then the $\mathfrak{a}$ defined by (v) is a left-ideal in $\mathfrak{b}_n$, and that it gives the original $\mathfrak{a}$ by the definition of (ii). In other words: (ii) and (v) establish a one-to-one correspondence between all linear subspaces $\mathfrak{A}$ of $P_{n-1}[\mathfrak{b}]$, that is all $\mathfrak{A} \epsilon L_n[\mathfrak{b}]$ on one side, and all left-ideals $\mathfrak{a}$ in $\mathfrak{b}_n$ on the other.

(vii) The definition (a), (b) in 2 for $\mathfrak{A} \cap \mathfrak{B}$ and $\mathfrak{A} \cup \mathfrak{B}$ can be used for $\mathfrak{a} \cap \mathfrak{b}$ and $\mathfrak{a} \cup \mathfrak{b}$ too: (a') $\mathfrak{a} \cap \mathfrak{b}$ = set-theoretical intersection of $\mathfrak{a}$, $\mathfrak{b}$, (b') $\mathfrak{a} \cup \mathfrak{b}$ = set of all $X + Y$, where $X \epsilon \mathfrak{a}$, $Y \epsilon \mathfrak{b}$. Now let $\mathfrak{a}$, $\mathfrak{A}$ correspond in the sense of (vi) (that is (ii), (v)), and $\mathfrak{b}$, $\mathfrak{B}$ too. Then $\mathfrak{a} \cap \mathfrak{b}$, $\mathfrak{A} \cap \mathfrak{B}$ correspond, as one sees by using (v), and $\mathfrak{a} \cup \mathfrak{b}$, $\mathfrak{A} \cup \mathfrak{B}$ correspond, as one sees by using (ii). In other words: (vi) establishes a *lattice-isomorphism* of $L_n[\mathfrak{b}]$ and of the lattice of all left-ideals in $\mathfrak{b}_n$.

(viii) Given an $\mathfrak{A} \epsilon L_n[\mathfrak{b}]$ we can obtain it as the linear subspace spanned by n vectors (n-uplets) $(x_{i1}, \ldots, x_{in})$ ($i = 1, \ldots, n$), that is the set of all $(\sum_{i=1}^{n} z_i x_{i1}, \ldots, \sum_{i=1}^{n} z_i x_{in})$, $z_1, \ldots, z_n \epsilon \mathfrak{b}$. (If fewer than n vectors $(x_{i1}, \ldots, x_{in})$ would do, dummies $(0, \ldots, 0)$ may be added.) This is clearly the $\mathfrak{A}$ (by (ii)) of the left ideal $\mathfrak{a}$ consisting of all ZX, $X = (x_{ij})$, Z arbitrary. $\mathfrak{a}$ is the *principal left-ideal* of X : $\mathfrak{a} = (X)_l$. So we see: Every left-ideal in $\mathfrak{b}_n$ is a principal left-ideal.

4. We can now modify the "coördinatization" statement of 2 as follows:

(*) The lattice of all left-ideals in $\mathfrak{b}_n$ is lattice-isomorphic to L_n. (Use (vii) in 3.)

Or just as well:

(**) The set of all principal left-ideals in $\mathfrak{b}_n$ is a lattice, and it is lattice-isomorphic to L_n. (Use (viii) in 3.)

Of course $\bigcap$, $\bigcup$ must be defined for left-ideals (and for principal left-ideals as well) by (a'), (b') in 3, (vii).

We will now attempt to "coördinatize" continuous geometries L_∞ by replacing $\mathfrak{d}_n$ in (*) or in (**) by more general rings $\mathfrak{R}$. It is reasonable to require that the not-necessarily-commutative but associative ring $\mathfrak{R}$ have a *unit* 1.

First we must decide whether (*) or (**) should be required, since in a ring $\mathfrak{R}$ which is not a $\mathfrak{d}_n$ all left-ideals need not be principal left-ideals. At any rate the greatest (smallest) element of L_∞ that is $1(0)$ must correspond to the greatest (smallest) left-ideal in $\mathfrak{R}$—which happens to be a principal left-ideal too—that is to $\mathfrak{R} = (1)_l$ ($(0) = (0)_l$). Now L_∞ is a *complemented* lattice, that is to each $a \epsilon L_\infty$ a $b \epsilon L_\infty$ with $a \bigcap b = 0$, $a \bigcup b = 1$ exists. Hence for each one of the corresponding left-ideals $\mathfrak{a}$ in $\mathfrak{R}$ a left-ideal $\mathfrak{b}$ in $\mathfrak{R}$ with $\mathfrak{a} \bigcap \mathfrak{b} = (0)$, $\mathfrak{a} \bigcup \mathfrak{b} = \mathfrak{R}$ must exist. The author proved in an earlier paper,[5] that such a left-ideal is necessarily a principal left-ideal (cf. R. R., Lemma 3), hence alternative (**) must be chosen. Furthermore $\mathfrak{R}$ must be such that for every principal left-ideal $\mathfrak{a}$ in $\mathfrak{R}$ a left-ideal $\mathfrak{b}$ in $\mathfrak{R}$ with $\mathfrak{a} \bigcap \mathfrak{b} = (0)$, $\mathfrak{a} \bigcup \mathfrak{b} = \mathfrak{R}$ exists. Such rings were called regular, loc. cit. above (cf. R. R., Definition 4), and investigated in some detail. The results which are particularly essential in the present situation are these:

If $\mathfrak{R}$ is regular, then the set $L_\mathfrak{R}$ of all principal left-ideals (and the set $R_\mathfrak{R}$ of all principal right-ideals as well) is a *complemented, modular lattice.* (Cf. R. R., Theorem II.)

If the "chain condition" or "minimum condition" (for left-ideals or right-ideals), familiar from abstract algebra, held in $\mathfrak{R}$, then regularity would be equivalent to "semi-simplicity" (cf. R. R., following Definition 4), hence by Wedderburn's theorem $\mathfrak{R}$ would be the direct sum of rings $\mathfrak{d}_n$. Thus the regular $\mathfrak{R}$ are just the generalization of "coordinatization" in the sense of 2, 3, beyond the domain of "chain conditions." The fact that our above considerations about L_∞ led so directly to these $\mathfrak{R}$ shows how appropriate the application of lattice-theoretical methods is, even in those parts of abstract algebra where the "chain-condition" no longer holds.

After these preliminaries we may generalize (**) somewhat further, and ask this question:

(‡) For which lattices L can a regular ring $\mathfrak{R}$ be found, such that L is lattice-isomorphic to the lattice $L_\mathfrak{R}$ of all principal left ideals of $\mathfrak{R}$?

And

(‡') For which lattices L is the above mentioned $\mathfrak{R}$ uniquely determined (up to ring-isomorphic changes)?

Since $L_\mathfrak{R}$ is complemented and modular, L must possess these properties too. We know from 2, 3 that for discrete (projective) geometries L_n with $n \geqq 4$, both questions (‡), (‡') are answered in the affirmative. For L_3

(plane geometry) the answer to (‡) is negative, as may be derived from the existence of "non-Desarguesian" plane geometries, while the answer to (‡′) is affirmative because the v. Staudt-algebra can be defined in a plane.[6] For $n = 1, 2$, even (‡′) is generally false. Hence we have generally affirmative answers for the L_n, except for (‡) if $n \leqq 3$, and for (‡′) if $n \leqq 2$.

Our main problem is now to answer (‡), (‡′) for the continuous geometries L_∞.

The Results. 5. We shall see that (‡), (‡′) are answered affirmatively for each L_∞ (to a certain extent without use of axiom VI, C. G., p. 96, which expresses "irreducibility"). Let us revert therefore to the general form of (‡), (‡′): L being any complemented and modular lattice. The exceptions found at the end of 4 for L_n's indicate that further restrictions on L are necessary. These are best expressed with the help of the following notions:

We say that a lattice L is of order m $(= 1, 2, \ldots)$ if m independent elements $\mathfrak{a}_i \epsilon L$, $i = 1, \ldots, m$, exist,[7] such that α) any two $\mathfrak{a}_i$, $\mathfrak{a}_j$ are perspective-equivalent (that is, possess a common inverse, cf. C. G., p. 97, Definition (1)), β) $\mathfrak{a}_1 \cup \ldots \cup \mathfrak{a}_m = 1$.

We say that an algebra $\mathfrak{R}$ is of order m, if m^2 "matrix units" $\gamma_{ij} \epsilon \mathfrak{R}$, $i, j = 1, \ldots, m$, exist, that is elements with the properties α') $\gamma_{ij}\gamma_{kl} \begin{cases} = \gamma_{il} & \text{for } j = k \\ = 0 & \text{for } j \neq k \end{cases}$, β') $\gamma_{11} + \ldots + \gamma_{mm} = 1$.

It is not difficult to verify that if $\mathfrak{R}$ is regular, then the lattice $L_\mathfrak{R}$ (or an L isomorphic to it) is of order m, if and only if $\mathfrak{R}$ is. The connection is given by $\mathfrak{a}_i = (\gamma_{ii})_l$,[8] while $\mathfrak{c}_{ij} = (\gamma_{ii} - \gamma_{ij})_l = (\gamma_{jj} - \gamma_{ji})_l$ is an axis of perspectivity for $\mathfrak{a}_i$ and $\mathfrak{a}_j$ (cf. C. G., p. 97). One shows furthermore without trouble: A discrete (projective) geometry L_n is of order m if and only if m is a divisor of n while a continuous geometry L_∞ is always of order m. Furthermore $\mathfrak{R}$ is of order m if and only if it is isomorphic to the mth order matrix-algebra $\mathfrak{S}_m$ over another ring $\mathfrak{S}$.

Our results are these:

Ad (‡): The answer to (‡) is affirmative if L is a complemented and modular lattice such that a) L possesses some order $\geqq 4$.

Ad (‡′): The answer to (‡′) is affirmative (in so far as $\mathfrak{R}$ exists at all) if L is a complemented and modular lattice such that a′) L possesses some order $\geqq 3$.

Since (a) implies (a′), we see: If (a) holds, then L is isomorphic to $L_\mathfrak{R}$ for one and (up to ring-isomorphic changes) only one regular ring $\mathfrak{R}$.

The necessity of conditions a), a′) is clear from the remarks made at the end of 4.

The proofs of these statements will be given in the detailed publication

referred to above. They are based, among other things, on a generalization of the construction of v. Staudt's "algebra of throws," as given in V.-Y., pp. 141–150 and 157.

6. We remarked in 5 that a continuous geometry L_∞ is of order m for every m, hence it fulfils (a), (a'). Hence it is isomorphic to the $L_\mathfrak{R}$ of a unique *regular ring* $\mathfrak{R}$.

L_∞, and thus $L_\mathfrak{R}$, is irreducible in the lattice sense (cf. C. G., p. 96, Remark 10). From this one infers easily that $\mathfrak{R}$ is irreducible in the usual sense, and hence the *center* $\mathfrak{Z}$ of $\mathfrak{R}$ is a division algebra (cf. R. R., Theorems 5 and 6). Thus a *commutative division algebra* $\mathfrak{Z}$ is associated with L_∞ in an invariant way. But while the invariant $\mathfrak{R}$ determined L_∞ (as L_∞ is isomorphic to $L_\mathfrak{R}$), $\mathfrak{Z}$ might not determine it. There are, however, some important cases where even $\mathfrak{Z}$ suffices to determine L_∞, and we shall discuss them in the next paragraph.

7. Let us first return to the L_n of 2, with $n \geqq 4$. We know from (**) in 4 that in this case L_n is isomorphic to an $L_n[\mathfrak{d}]$, and $\mathfrak{R} = \mathfrak{d}_n$. The center $\mathfrak{Z}$ of $\mathfrak{R} = \mathfrak{d}_n$ is therefore isomorphic to the center of $\mathfrak{d}$.

Now L_n (that is $L_n[\mathfrak{d}]$) determines $\mathfrak{d}$ up to an isomorphism, and is determined by $\mathfrak{d}$ in the same sense. Hence the center of $\mathfrak{d}$, that is $\mathfrak{Z}$, does not determine L_n: $\mathfrak{d} = \mathfrak{d}_r$ = system of all real numbers, and $\mathfrak{d} = \mathfrak{d}_q$ = system of all real quaternions, give anisomorphic geometries $L_n[\mathfrak{d}]$, but they have the same center $\mathfrak{Z} = \mathfrak{d}_r$.

Hence $\mathfrak{Z}$ is not sufficient to characterize an L_n, $n \geqq 4$.

Consider now the construction of E. C. G., pp. 103–105. We write $\mathfrak{d}$ for the $\mathfrak{Z}$ loc. cit. (which was a not-necessarily-commutative division-algebra), and $L_\infty[\mathfrak{d}]$ for $L^{(\infty)}[\mathfrak{Z}]$. $L_\infty[\mathfrak{d}]$ is a continuous geometry; so it determines a regular ring $\mathfrak{R}$ in the sense of 5 and 6, and the center of $\mathfrak{R}$ is our $\mathfrak{Z}$. (Not the $\mathfrak{Z}$ of E. C. G., cf. above!) It is not difficult to show that $\mathfrak{Z}$ is isomorphic to the center of $\mathfrak{d}$. Hence it seems plausible that $\mathfrak{Z}$ will again not determine $L_\infty[\mathfrak{d}]$. However, we know that $\mathfrak{Z}$ is an isomorphism-invariant of $L_\infty[\mathfrak{d}]$, while we have not shown the same thing concerning $\mathfrak{d}$. It is remarkable therefore that we can show:

Restrict $\mathfrak{d}$ to division-algebras which are of finite order over their center.

Then two $L_\infty[\mathfrak{d}]$ are (lattice-) isomorphic, if and only if the centers of their $\mathfrak{d}$ are (ring-) isomorphic. That is: If and only if their $\mathfrak{Z}$ are (ring-) isomorphic.

The necessity follows, of course, from the invariance of $\mathfrak{Z}$, while the sufficiency is established by algebraic considerations, mainly with the help of a theorem of T. Skolem and E. Noether.

Thus $L_\infty[\mathfrak{d}_r]$ and $L_\infty[\mathfrak{d}_q]$ are isomorphic, while the $L_n[\mathfrak{d}_r]$ and $L_n[\mathfrak{d}_q]$ are not! But they are not isomorphic to $L_\infty[\mathfrak{d}_c]$, $\mathfrak{d}_c$ = System of all complex numbers, since then $\mathfrak{Z} = \mathfrak{d}_c$.

As the $L_\infty[\mathfrak{d}]$ are thus characterized by the necessarily commutative $\mathfrak{Z}$,

one might say: L_n, $n = 1, 2, 3, \ldots, \infty$, becomes automatically Desarguesian when n becomes $\geqq 4$, and it becomes Pascalian when n becomes $= \infty$.

Further Investigations. 8. We shall discuss in further publications several questions which could not be touched here, namely:

The algebraic properties of those regular rings $\mathfrak{R}$ for which $L_{\mathfrak{R}}$ is a continuous geometry. They are characterized by the existence of a "numerical rank" ($\geqq 0$, $\leqq 1$) for the $\xi \epsilon \mathfrak{R}$—equivalent of the "numerical dimension" for the $\mathfrak{a} \epsilon L_{\mathfrak{R}}$.

The effects the existence of a dualizing complementation-operation in $L_{\mathfrak{R}}$ has on $\mathfrak{R}$.[9] It turns out to be equivalent to the existence of an operation in $\mathfrak{R}$ which possesses the essential properties of a "Hermiteian adjoint."

If $\mathfrak{Z}$ is the quotient-algebra of ring $\mathfrak{T}$, which is to be considered as the "ring of integers" in $\mathfrak{Z}$, then it is possible to define the notion of an integer in $\mathfrak{R}$, and investigate the arithmetical properties of $\mathfrak{R}$, provided that $L_{\mathfrak{R}}$ is a continuous geometry. (Observe that this cannot be done for the infinite [bounded] matrices in Hilbert space, owing to the absence of a "characteristic equation.")

[1] J. v. Neumann, "Continuous Geometry," *Proc. Nat. Acad. Sci.*, **22**, 92–100 (1936), and "Examples of Continuous Geometries," *Ibid.*, 101–108, to be quoted as C. G. and E. C. G., respectively.

[2] The method which we will use is not the one sketched at the end of E. C. G. It is essentially more powerful.

[3] That is: Dimension $= n - 1 \geqq 3$. So the geometry L_n is certainly "Desarguesian."

[4] O. Veblen and W. Young, "Projective Geometry," vols. I and II, Boston 1910 and 1918. Vol. I will be quoted as V.-Y.

[5] J. v. Neumann, "On Regular Rings," *Proc. Nat. Acad. Sci.*, **22**, 707–713 (1936), to be quoted as R. R.

[6] Only the proof of the associative law of multiplication requires spatial constructions, but this is not required for the isomorphism-considerations.

[7] The $\mathfrak{a}_i$, $i = 1,\ldots,n$ are independent, if $(\mathfrak{a}_1 \cup \ldots \cup \mathfrak{a}_i - {}_1 \cup \mathfrak{a}_i + {}_1 \cup \ldots \cup \mathfrak{a}_n) \cap \mathfrak{a}_i = 0$ for $i = 1, \ldots, n$.

[8] $(\alpha)_l$ is the principal left-ideal of $\alpha \epsilon \mathfrak{R}$: the set of all $\xi \alpha_\lambda$ $\xi \epsilon \mathfrak{R}$.

[9] That is an operation $\mathfrak{a}'$ for the $\mathfrak{a} \epsilon L_{\mathfrak{R}}$, such that $(\mathfrak{a} \cup \mathfrak{b})' = \mathfrak{a}' \cap \mathfrak{b}'$, $(\mathfrak{a} \cap \mathfrak{b})' = \mathfrak{a}' \cup \mathfrak{b}'$, $\mathfrak{a}'' = \mathfrak{a}$, $\mathfrak{a} \cup \mathfrak{a}' = 1$, $\mathfrak{a} \cap \mathfrak{a}' = 0$.

ON THE LAW FOR MINIMAL DISCRIMINATION OF INTENSITIES. I

BY W. J. CROZIER AND A. H. HOLWAY

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY

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I. The sensory discrimination of intensities is measured by obtaining differentiating response to two just distinguishable intensities of an excitatory agency. The quantitative data of discrimination are the materials for the theory of sensory discrimination. It has also been held, or taken for granted, that they are to be interpreted in terms of peripheral sensory mechanisms. The fact is, however, that the really significant and characteristic properties of these data are essentially nonspecific with reference to their receptor-origins. A general law describing these properties has therefore important consequences for the use of the data of sensorial discrimination. We shall illustrate such a general rule by means of a variety of examples from recent experimentation. It is to be shown that the properties of the marginally discriminable interval of intensity ΔI, where $\Delta I = \tilde{I}_2 - I_1$, are determined by probability considerations[1] which are completely independent of specific structural or other properties of the receptor field.[2] The demonstration of this fact provides basic conditions which must be satisfied by any proposed construction from such data of the laws of sensory effect as a function of intensity. The existing constructions do not meet these requirements.[3]

The respects in which the demonstrable properties of ΔI can be shown to possess a statistical basis depend for their recognition upon the use of homogeneous data.[4,1] That these may be obscured in data which are in one way or another non-homogeneous is easily verified experimentally. It follows that attempted analysis of non-homogeneous measurements is likely to be highly unprofitable and even misleading.

II. A direct proportionality has been shown to exist, in homogeneous series of measurements, between ΔI_m for visually aroused responses of various lower animals and the variability of $\tilde{I}_2$.[4] Precisely the same rule holds for human visual determinations of ΔI_m as a function of I. Regardless of the transition from rod- to cone-excitation, ΔI and σ_{I_2} $(= \sigma_{\Delta I})$ are in simple proportion.[5] It does not affect the form of this relationship (1) if the method of comparison be that of simultaneous or of successive exposure, (2) if ΔI_m for given I_1 is altered by changing the area of the test-patch, (3) whether a "surround" or an artificial pupil is used, (4) if the experiment be made by the "method of limits" or by that of "average error" or (5) if the ΔI_m is obtained by increasing or decreasing I_2.[6] There

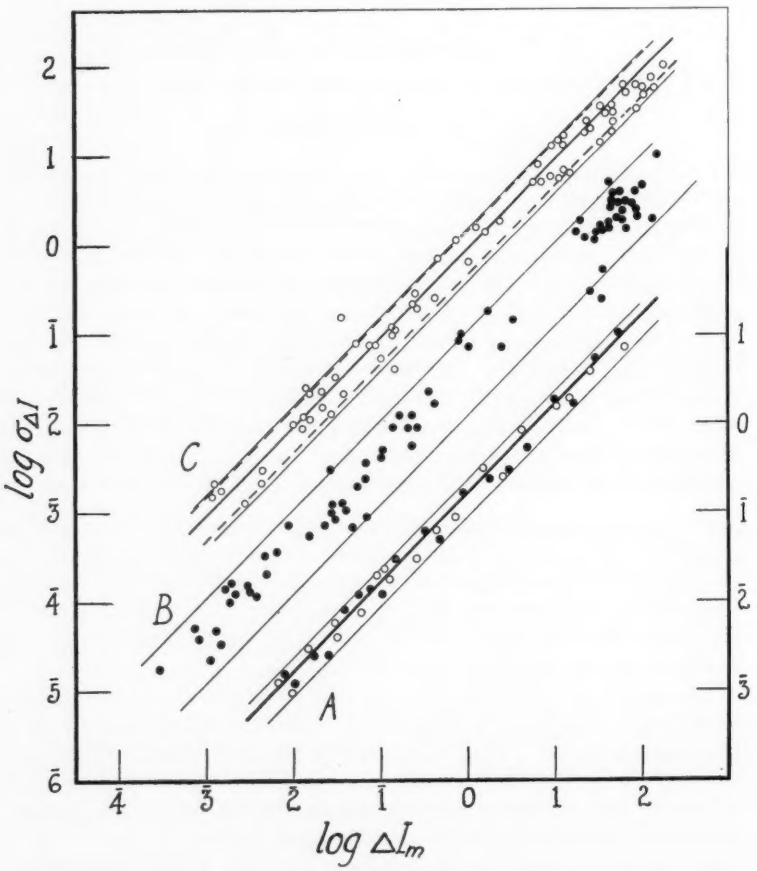

FIGURE 1

Vision—Mean ΔI(ΔI_m, millilamberts) is directly proportional to the root-mean-square departure ($\sigma_{\Delta I}$). Graph *A* is from homogeneous data by Holway[5] using the method of limits (simultaneous comparison) for one observer: the open circles denote $\sigma_{\Delta I}$ for increasing I_2; the solid circles, $\sigma_{\Delta I}$ for decreasing I_2. The central line has a slope = 1, and it bisects arithmetically the vertical distance between the enclosing limits. Plots *B* and *C* are from data of Holway and Hurvich,[6] using the method of limits (successive comparison), for two observers. Scale for *A* is at right; ordinates for *C* have been multiplied by 10. All lines have slope = 1.

Curve *C* illustrates the procedure (see text) in which a mean line, and mean $\pm\sigma\sigma_{\Delta I}$ are fitted.

are quantitative differences between the results in these various cases, which are interesting and important, but the law of the result is in each case that ΔI_m and σ_{I_1} are directly proportional. Figure 1 contains illustrations. The relationship to the identical law for flicker has been discussed elsewhere.[7]

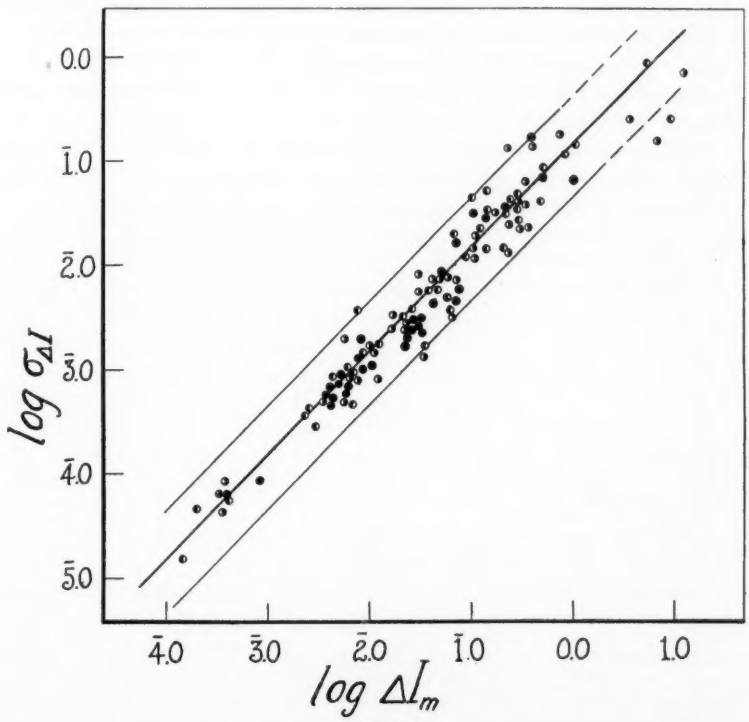

FIGURE 2

Audition—**Showing that** $\sigma_{\Delta I}$ is proportional to ΔI_m (bars) for homogeneous data obtained by Upton and Holway[9,10] using the method of limits. (The precise positions of the five points at the right, taken at very high intensities (I_1), are of lesser reliability, owing to the uncertainty as regards the shape of the calibration curves for the ear phones in this region.) Three levels of intensity were employed and exposure-time was varied. The half-shaded circles are for monaural presentation: those shaded on the left are for the left ear; those on the right, for the right ear. The solid circles stand for values secured under the conditions of binaural stimulation.

The rule applies equally in auditory intensity-discrimination.[8] It continues to hold when, at fixed I_1, exposure-time also enters as a variable and ΔI systematically changes.[9] It is not disturbed by the use of binaural or of monaural stimulation[10] (Fig. 2).

The interdependence of ΔI_m and $\sigma_{\Delta I}$ is apparent in various other sensory fields. We take an illustration from an extensive investigation of the properties of ΔW in the judgment of differences in weights[11] (Fig. 3). The form of the relationship is independent of the mode of lifting, of W_1, and of the frequency of arm movements, even though when frequency is increased ΔW for fixed W_1 goes through a minimum.[12] The relationship is quite apparent in data from studies of other modes of sensitivity for which it is not possible to work so accurately and over so wide a range of I[13] (Fig. 4); neater examples are given by data for deep pressure from Wundt's laboratory.[15]

III. In a homogeneous body of determinations of ΔI_m as a function of I_1 each value of ΔI_m is associated with a $\sigma_{\Delta I}$; and each $\sigma_{\Delta I}$ carries with it a σ_{σ}, $= k\sigma_{\Delta I}$. The width of the band shown upon a log-log plot of ΔI_m vs. $\sigma_{\Delta I}$ is therefore constant, with equivalent intrinsic precision in the determinations of $\sigma_{\Delta I}$ at all points, and is proportional to $k\sigma_{\Delta I}$; it therefore measures σ_{σ}. This width supplies a means of estimating, by its reciprocal, the comparative precision of different procedures for determining ΔI_m with the same observer. It also gives a basis for the comparison of the intrinsic precision of judgment for different observers, using the same methods. These estimates of precision are independent of I_1. When an arithmetic plot is used (Figs. 3, 4), the points are necessarily distributed in a fan. The principles of curve fitting which apply here are similar to those involved in the reduction of data upon temperature characteristics.[14]

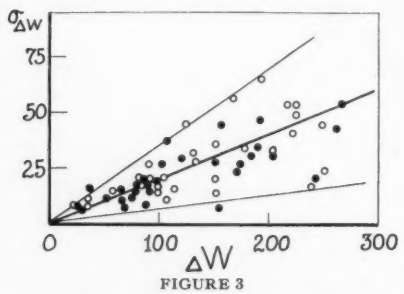

FIGURE 3

Kinesthesis (lifted weights)—Showing that $\sigma_{\Delta W}$ is proportional to ΔW (grams). Homogeneous data from Holway and Hurvich[11] using the method of limits (simultaneous comparison; continuous change; direction of increase) for one observer. The open circles denote values for active procedure (weights rhythmically elevated and lowered at a rate of "30 per minute"); the closed circles are for passive procedure. The central line vertically bisects the enclosing limits, and has an equal number of points on either side of it.

IV. Plots such as those in Figures 1, 2, 3 show that the proportionality between ΔI_m and $\sigma_{\Delta I}$ is simple and direct. If $\sigma_{\Delta I}$ could be obtained for a large number of successive sets of determinations of ΔI_m having exactly the same magnitude, $\sigma_{\Delta I}$ would be normally distributed. We can test this by reducing the data in, for example, Figure 1*C* to a condition in which the ordinary considerations of statistical theory apply. These considerations do not apply directly when σ is proportional to the mean—

a fact which must not be overlooked. The reduction is obtained by projecting each point to an ordinate, on a path with slope = 1. The line of slope = 1 which passes through the arithmetic mean ($\bar{\sigma}_{\Delta I}$) of the projected $\sigma_{\Delta I}$'s should then divide the assemblage of plotted points into two equally numerous groups; the line through mean ΔI for levels of $\sigma_{\Delta I}$ does not. In non-homogeneous data this will not be true, in general, since in that case the ordinate projection of the line of $\bar{\sigma}_{\Delta I}$ as well as $\sigma_{\sigma_{\Delta I}}$ will itself be distributed in some fashion, and the various sets of homogeneous points will be more or less haphazardly intermingled. For a homogeneous set, use can be made of the theorem of Tchebycheff to establish the marginal enclosing lines, since mean $\bar{\sigma}_{\Delta I} \pm \sigma_{\bar{\sigma}_{\Delta I}}$ must enclose more than 75 *per cent* of the observations. In Figure 1*C*, the dashed lines through $\bar{\sigma}_{\Delta I} \pm \sigma_{\bar{\sigma}_{\Delta I}}$ enclose 80 *per cent* of the points. Reciprocally, if the data are sufficiently numerous, marginal lines may without violence be drawn by inspection, and the central line dividing the region between into arithmetically equal parts should divide the observations equally.

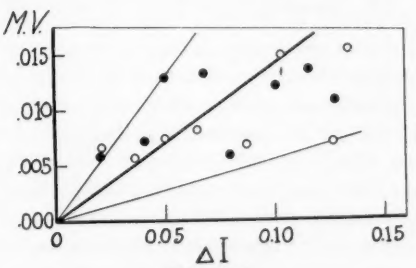

FIGURE 4

Cutaneous pressure—Showing that M. V.$_{\Delta I}$ is proportional to ΔI (gm./mm.). Homogeneous data from Gatti and Dodge,[13] obtained for the tip of the little finger under conditions of rapid loading with microscopic stimuli and using the method of limits for one observer. The open circles denote increasing I_2; the solid circles, decreasing I_2. The central line vertically bisects the enclosing limits, and has an equal number of points on either side of it.

From this relationship it follows that a given level of $\sigma_{\Delta I}$ is not associated with a certain mean value of ΔI, but that a certain level of ΔI_m is governed by a given mean $\sigma_{\Delta I}$ (i.e., by a given $\sigma_{\Delta I} \pm \sigma_{\sigma_{\Delta I}}$). The mean value of ΔI obtained for a given I_1 is determined by the test-organism's capacity for variation of performance. The direct experimental proof of this is obtained by tests into which we need not now go. The propriety of the calculation of the quantitative properties of ΔI on this basis has been demonstrated. The significance is that the law for intensity-discrimination is primarily to be a law for the "capacity to vary performance"; this capacity for variation of performance is responsible for the fluctuation of intensity (I_2) required to produce the index-response.

V. The properties of ΔI_m indicate that $\tilde{I}_2$ is discriminated from I_1 in terms of the (variable) effect of I_1 and the effect produced by an exposure to an I_2. The variability of I_2 is due to the fact that the organism's ca-

pacity to be excited fluctuates. A mean value of I_2 gives $\tilde{I}_2 - I_1 = \Delta I_m$. The recognition of I_2 as different from I_1 requires that the effect to be produced by recognizably different I_2 shall be statistically far enough removed from the central tendency of the effects produced by I_1, otherwise the probability of the occurrence of the index-response will not be great enough to give a detectable result. The magnitude of ΔI_m is therefore determined by the variability. This is particularly striking when illuminated area of retina is increased: the total sensory effect is then greater, but $\sigma_{\Delta I}$ and ΔI_m decrease;[6] similarly, in audition, when I_1 is delivered to the two ears, the subjective effect is reported as having "twice the loudness" resulting when I_1 is delivered to one ear alone, but $\sigma_{\Delta I}$ and ΔI_m decrease; whereas with constant area of sensory field $\sigma_{\Delta I}$ (and ΔI_m) increases with I_1.[12]

VI. *Summary.*—Sensory discrimination of two just recognizably different intensities I_1 and $\tilde{I}_2$ is governed by the fact that the just discriminable ΔI is directly proportional to, and determined by, σ_{I_2}. The properties of the data of sensory discrimination arise from the essentially statistical (i.e., probability) character of the basis for comparison between the effects due to I_1 and the variable capacity of the organism to give a statistically distinguishable effect under the action of a compared I_2. The governance of ΔI by σ_{I_2} is independent of any specific properties of a particular peripheral or central sensory mechanism.

[1] Crozier, W. J., *Proc. Nat. Acad. Sci.*, **22**, 412 (1936). $\tilde{I}_2$ = "I_2 adjusted."

[2] Upton, M., and Crozier, W. J., *Proc. Nat. Acad. Sci.*, **22**, 417 (1936).

[3] Crozier, W. J., and Pincus, G., *Jour. Gen. Physiol.*, **11**, 789 (1927–28).

[4] Crozier, W. J., *Jour. Gen. Physiol.*, **19**, 503 (1936).

[5] Holway, A. H., *J. O. S. A.* (in press).

[6] Holway, A. H., and Hurvich, L. M., *Jour. Psychol.* (in press).

[7] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.* (in press) (1936–37).

[8] Upton, M., and Crozier, W. J., *Proc. Nat. Acad. Sci.*, **22**, 417 (1936).

[9] Upton, M., and Holway, A. H., *Proc. Nat. Acad. Sci.*, (in press).

[10] Upton, M., and Holway, A. H., *Proc. Nat. Acad. Sci.*, (in press). This has an important bearing upon the problem of comparing results for differential sensitivity and those for the bisection of "sense-distances."

[11] Holway, A. H., Harvard University Thesis, Harvard College Library, 65 pp. (1936); cf. also, Holway, A. H., and Hurvich, L. M., *Jour. Psychol.*, (in press) (1936); and Holway, A. H., and Crozier, W. J., *in preparation.*

[12] Holway, A. H., Smith, J., and Zigler, M. J., *Jour. Psychol.* (in press).

[13] Gatti, A., and Dodge, R., *Arch. ges. Psychol.*, **69**, 405 (1929).

[14] Crozier, W. J., *Déterminisme et variabilite*, Paris, Hermann, 56 pp. (1935).

[15] Stratton, G. M., *Philos. Stud.*, **12**, 525 (1896).

ON THE PSYCHOPHYSICS OF HEARING. I. MONAURAL DIFFERENTIAL SENSITIVITY AND EXPOSURE-TIME

BY MORGAN UPTON AND ALFRED H. HOLWAY

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY

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I. *Introduction.*—In experiments upon differential sensitivity to acoustical intensities, very little emphasis has been placed upon the control of the factor of time. It has even been asserted that the phenomenon of adaptation was not characteristic of the auditory mechanism.[6] In order to obtain psychophysiologically useful functions, however, the factor of time must be considered. The observations presented here demonstrate the fact that differential sensitivity ($1/\Delta I$) varies lawfully as a function of time.

II. A special form of the Method of Limits was used; the procedure involved monaural presentation and continuous change in the direction of increase. Observations made under this type of method and procedure are obtained rapidly, are reproducible and are optimally useful from the standpoint of psychophysiological interpretation.

The source of sound was a Type 613 General Radio Beat Frequency Oscillator. The output of the oscillator was amplified and led to a pair of Type 509 W Western Electric headphones.[4] A volume control on the amplifier afforded adequate control of the energy actuating the headphones. The voltage at the phones was measured by using a high impedance calibrated variable attenuation network. The network was calibrated so that the voltage at its input terminals was indicated on a suitable dial when the voltage at the output terminals was equal to one millivolt. An amplifier voltmeter, set at a gain of one thousand, was used as an indicating instrument. When the reading on the voltmeter was one volt the attenuator indicated the voltage at the phone terminals. Thus the meter was used as a null instrument and the system afforded a continuous range voltmeter, capable of measuring voltages from 0.001 to 100 volts.

The acoustic output of the telephones was determined as a function of the impressed voltage by means of a standardized microphone. This relationship was found to be linear over the range of voltages used in this experiment. The calibration curves will be published in a later paper.

III. To determine the functions relating differential sensitivity to time, 7 values were selected on the temporal continuum (1, 3, 10, 20, 40, 90, 120 secs.) at 3 levels of intensity (I = 0.05, 0.25 and 1.25 bars) for each ear. The frequency was 800 cycles. Determinations for the three

TABLE 1

MONAURAL ΔI-VALUES OBTAINED AT STATED LEVELS OF INTENSITY (I, IN BARS) AFTER SPECIFIED EXPOSURE TIMES (t, IN SECONDS) FOR EACH EAR OF OBSERVER NO. 1. EVERY ΔI-VALUE IS AN AVERAGE OF 5 MEASUREMENTS; σ IS THE ROOT-MEAN-SQUARE VARIATION OF THE INDIVIDUAL MEASUREMENTS

	$I = 0.05$				$I = 0.25$				$I = 1.25$			
	LEFT		RIGHT		LEFT		RIGHT		LEFT		RIGHT	
t	ΔI	σ	ΔI	σ	ΔI	σ	ΔI	σ	ΔI	σ	ΔI	σ
1	0.0224	0.00343	0.0315	0.00638	0.1275	0.0242	0.0995	0.0137	0.859	0.135	0.796	0.209
3	0.0143	0.00200	0.0171	0.00263	0.0740	0.0051	0.0704	0.00373	0.530	0.101	0.421	0.089
10	0.00944	0.00164	0.0116	0.00163	0.0612	0.00864	0.0653	0.00531	0.301	0.0501	0.252	0.0284
20	0.00816	0.00405	0.0102	0.00180	0.0459	0.00477	0.0497	0.00823	0.293	0.0419	0.184	0.0375
40	0.00727	0.000510	0.00778	0.000845	0.0421	0.00649	0.0365	0.00153	0.153	0.0161	0.110	0.0130
90	0.00701	0.000901	0.00612	0.00216	0.0321	0.00903	0.0303	0.00316	0.148	0.0585	0.117	0.0250
120	0.00536	0.000910	0.00599	0.000510	0.0245	0.00187	0.0250	0.00297	0.150	0.0355	0.110	0.0163

levels of intensity were taken on three successive days. The results obtained for Observer No. 1 are presented in table 1.

IV. That differential sensitivity to sound is clearly a specific, reproducible function of time is shown graphically in figure 1. Each half-shaded circle in the figure represents an average of five measurements. Those shaded on the left represent data for the left ear; those on the right, for the right ear. The broken lines are fitted to the arithmetic averages at each level of intensity. The slopes of these functions apparently vary with the intensity-level. The exact nature of the relation between $d(\Delta I)/dt$ and I will be revealed by a more detailed investigation upon a given observer throughout a wide range of intensities. The relationship which exists between ΔI and t in this experiment, however, may be expressed by the equation

$$\log \Delta I = -K \log t + C,$$

where ΔI is the just noticeable increment in intensity and K and C are constants. In terms of differential sensitivity:

$$\log (1/\Delta I) = K \log t + C'.$$

These constants are as yet quite arbitrary. Accordingly the equation must be provisional.

Discussion.—Adrian has shown that under conditions of "continued stimulation" the frequency of nervous impulses in a single fibre decreases as a function of time.[1] If this phenomenon is a characteristic of the fibres

constituting the acoustic paths (as is quite possible),[5] then some function of the sort illustrated in figure 1 might be expected. Such an expectation, however, would necessarily entail a theory of differential sensitivity. An explanatory theory of differential sensitivity (one which is coherent with physiological fact) has been suggested.[2] It asserts that $1/\Delta I$ varies directly with the number of elements (= number of impulses per unit of time) available for the discrimination in question. This suggestion is in general consistent with the established facts of differential

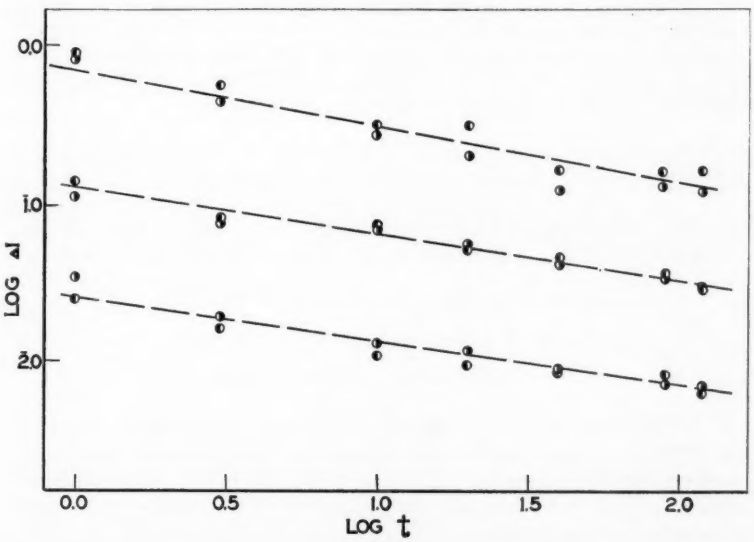

FIGURE 1

Just noticeable increments in intensity (ΔI) as a function of exposure-time (t, in seconds) for three levels of intensity (I = 0.05, 0.25 and 1.25 bars). The abscissa values indicate the interval of time during which the subject was exposed to the tone before he attempted the required adjustment. Each half-shaded circle is an average of 5 measurements. The circles shaded on the left are for the left ear; those on the right, for the right ear. For monaural presentation, ΔI varies directly with I, and inversely with t.

sensitivity,[3] and is definitely supported by the results secured in this experiment.

A more detailed discussion of these results will appear elsewhere.

Summary.—The necessity for the control of the temporal factor in auditory experiments has been demonstrated. The relation existing between differential sensitivity and exposure-time has been determined at 3 levels of intensity for durations ranging from 1 to 120 seconds (frequency = 800 c. p. s.). Differential sensitivity to sound varies directly with

exposure-time. A physiological explanation is advanced to account for this phenomenon.

[1] Adrian, E. D., *The Basis of Sensation*, W. W. Norton Co., New York, 1928, 122 pp.

[2] Holway, A. H., and Hurvich, L. M., 1937, "A Theory of Differential Sensitivity," *Jour. Psychol.* (in press).

[3] Holway, A. H., and Pratt, C. C., "The Weber-Ratio for Intensitive Discrimination," *Psychol. Rev.*, **43**, 322–340 (1936).

[4] Upton, M., "Differential Sensitivity in Sound Localization," *Proc. Nat. Acad. Sci.*, **22**, 409–412 (1936).

[5] Derbyshire, A. J., and Davis, H., "The Action Potentials of the Auditory Nerve," *Amer. Jour. Physiol.*, **113**, 476–504 (1935).

[6] However, for a demonstration of the fact that adaptation is a pronounced and lawful phenomenon of hearing, see v. Békésy, G., "Zur Theorie des Hörens, etc.," *Physik. Zeitschr.*, **30**, 115–125 (1929).

ON THE PSYCHOPHYSICS OF HEARING. II. BINAURAL DIFFERENTIAL SENSITIVITY AND EXPOSURE-TIME

BY MORGAN UPTON AND ALFRED H. HOLWAY

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY

Communicated December 3, 1936

I. Psychophysical results have been obtained concerning the relationship between exposure-time and differential sensitivity to monaurally presented sound-intensities.[3] Differential sensitivity ($1/\Delta I$) was found to vary lawfully with exposure-time. In this paper, results for binaural stimulation are considered.

II. The method, procedure and apparatus have been described.[3] To determine the function connecting differential sensitivity with time, just noticeable increments in intensity were measured for the same durations of exposure, and at the same levels of intensity as were employed in the monaural determinations. Moreover, the binaural and monaural determinations for a given level of intensity were taken on the same day, and on the same observers. The results for Observer No. 1 are given in table 1.

In the binaural procedure, the acoustical "intensity" (= number of dynes per square centimeter) was in each instance the same as that employed in the monaural experiment. For binaural stimulation, however, the total amount of excitation was perhaps *twice* that for monaural stimulation. The ΔI-values obtained under these two sets of conditions need not agree. Relative to the magnitude of the monaural determinations, there exist three mutually exclusive hypotheses which might be invoked to predict the magnitude of the measurements secured in the

TABLE 1

MEAN VALUES OF ΔI FOR BINAURAL PRESENTATION, OBTAINED AFTER SPECIFIED TIMES OF EXPOSURE (t IN SECONDS) AND AT STATED LEVELS OF INTENSITY (I IN BARS). EACH VALUE OF ΔI IS THE AVERAGE OF FIVE MEASUREMENTS; σ REPRESENTS THE ROOT-MEAN-SQUARE VARIATION OF THE INDIVIDUAL MEASUREMENTS

	I = 0.05		I = 0.25		I = 1.25	
t	ΔI	σ	ΔI	σ	ΔI	σ
1	0.0119	0.00118	0.0816	0.00670	0.541	0.0836
3	0.00880	0.00215	0.0671	0.00416	0.413	0.0210
10	0.00612	0.000864	0.0513	0.00657	0.235	0.0408
20	0.00548	0.000954	0.0377	0.00191	0.150	0.0336
40	0.00548	0.000765	0.0337	0.00308	0.110	0.0357
90	0.00510	0.000806	0.0303	0.00306	0.0765	0.0180
120	0.00434	0.000567	0.0232	0.00301	0.0587	0.00846

present experiment: (1) Since the total excitation is "doubled," it could be expected that ΔI would increase (cf. the principle involved in the Weber-function). (2) However, the observer might equally well be expected in each presentation to avail himself of his more sensitive "ear." In this

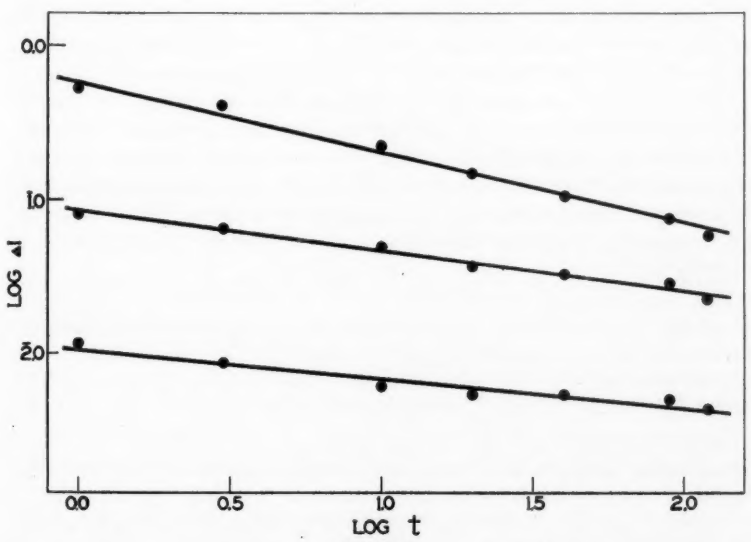

FIGURE 1

Just noticeable increments in intensity (ΔI) as a function of exposure-time (t, in seconds) for three levels of intensity (I = 0.05, 0.25 and 1.25 bars). The abscissa values indicate the interval of time during which the subject was exposed to the tone before he attempted the required adjustment. Each point is an average of five measurements made for binaural stimulation. ΔI varies directly with I, and inversely with t

event, the binaural ΔI-values should coincide with those obtained monaurally for the more sensitive ear. (3) If the theory of differential sensitivity[1,3] adopted to account for the monaural results is of specific validity, then the ΔI-determinations for binaural presentation should be definitely smaller than the lower of the two monaural values obtained at a given time and level of intensity. The present experiment was devised to evaluate these three mutually exclusive possibilities.

The results are exhibited graphically in figure 1. Each shaded circle is an average of 5 measurements (Observer No. 1). The data are homogeneous.[5] In fitting the solid lines to the results, the highest values of ΔI received least "weight" (cf. table 1). Binaural differential sensitivity to sound is seen to be a specific function of exposure-time. The law interrelating ΔI and t for binaural presentation is essentially identical in form with that for monaural presentation. For the binaural situation, however, the values of ΔI at each level of intensity are definitely smaller than those obtained in the monaural situation.[6] Possibilities (1) and (2) as stated above must accordingly be rejected. Differential sensitivity seems to vary directly with the number of elements[1] (= impulses per unit of time) available for discrimination. This theory makes differential sensitivity a measurable capacity of the "pre-efferent" nervous system,[1,4] a capacity that is lawfully conditioned by peripheral events.

Summary.—The relationship between binaural differential sensitivity and exposure-time has been determined for three levels of intensity. Differential sensitivity $(1/\Delta I)$ increases as a function of exposure-time. Moreover, differential sensitivity is found to be greater for binaural than for monaural stimulation. Further support for a physiological theory of differential sensitivity[1,3] is adduced from these results.

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STIMULATIVE AND INHIBITIVE INDUCTION IN THE DEVELOPMENT OF PRIMARY AND SECONDARY SEX CHARACTERS*

BY EMIL WITSCHI

DEPARTMENT OF ZOÖLOGY, STATE UNIVERSITY OF IOWA

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It is a well established fact that in the development of the vertebrate gonad the cortex functions as an inductor of ovarian differentiation and the medulla as an inductor of testicular differentiation. Embryologically, sex is determined on the basis of a competition between these two inductors, each of which stimulates differentiation of one sex and tends to prevent the development of the other.

A closer analysis of the inductor activity indicates, furthermore, that the visible morphological differentiations are evoked by special chemical substances which are produced and released by the inductors. This assumption was probably first suggested and supported by F. R. Lillie[1] in his classical studies on the cattle free-martins. The now equally well established fact that in primates a similar exchange of blood between male and female embryos does not interfere with normal sex development cannot reduce the importance of the free-martin case; though it proves that the mechanism of induction deserves a more detailed investigation.

Evidently cortex and medulla produce different inductive substances; it has been proposed to designate them as *cortexin* and *medullarin*. In the experiments to be described now, we have investigated the question of whether the stimulative and the inhibitive inductions are due to one or to two (or more) substances. The evidence points to the separate existence of a stimulative and of an inhibitive medullarin. Using the technique of Born[2] we made parabiotic pairs of salamanders, and observed the effects of inductive substances which are transmitted from one twin into the other. In the case represented in figure 1 an Ambystoma maculatum female is loosely attached to an A. tigrinum male by a strand of tissue between the right gill arches. The maculatum female proves to be nearly sterile. As in other similar combinations the sex glands are reduced to small vestiges, without ovarial differentiation (compare Fig. 2C). This proves that the blood passing through the narrow connection has carried enough medullarin into the female to suppress cortical development. On the other hand no sign of testicular differentiation is visible in the medulla. Stimulation of testicular differentiation is restricted to the gonad of the tigrinum male while inhibition of ovarial differentiation spreads also into the maculatum female.

In another series of twins it was observed that males with hermaphrodite

FIGURE 1

Pair of parabiotic twins. The large A. tigrinum member is a male, the small A. maculatum co-twin is a female free-martin. They are connected by a narrow strand of tissue between the gill arches. Age 5 months. $\times 1/2$.

tendencies do not emit the inhibitive medullarin in appreciable amounts (Witschi[3]), indicating a wider quantitative variability in the inhibitive than in the stimulative medullarin. In a third series two males which differ in developmental speed were united. The fact that the pace of the later and more slowly differentiating twin is not speeded up, proves most directly that stimulative medullarin is not transmitted from one twin into the other (Witschi[4]). Experimental evidence leads, therefore, to the conclusion that in salamanders the medulla produces two inductive substances. The first one which stimulates testicular differentiation, produces reactions only within the gonad. Like many other substances which induce embryonic differentiations, it seems to diffuse very slowly and only by direct contact through the tissues. The second one, which

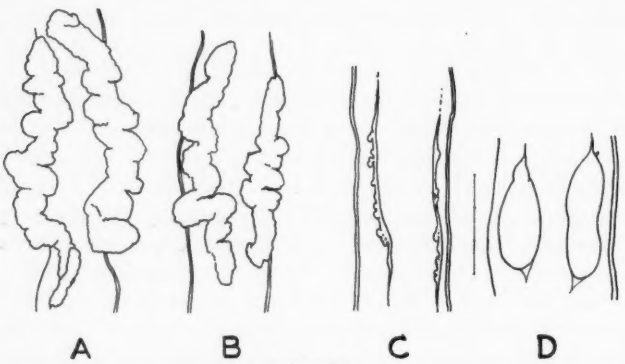


FIGURE 2

Sex glands of a female pair (A, B) and a heterosexual pair (C, D) of salamanders ($17\,1/2$ and $13\,1/2$ months old). A, B, normal ovaries; C, vestigial sex glands of the female (free-martin) in parabiosis with a male; D, normal testes. $\times 5$.

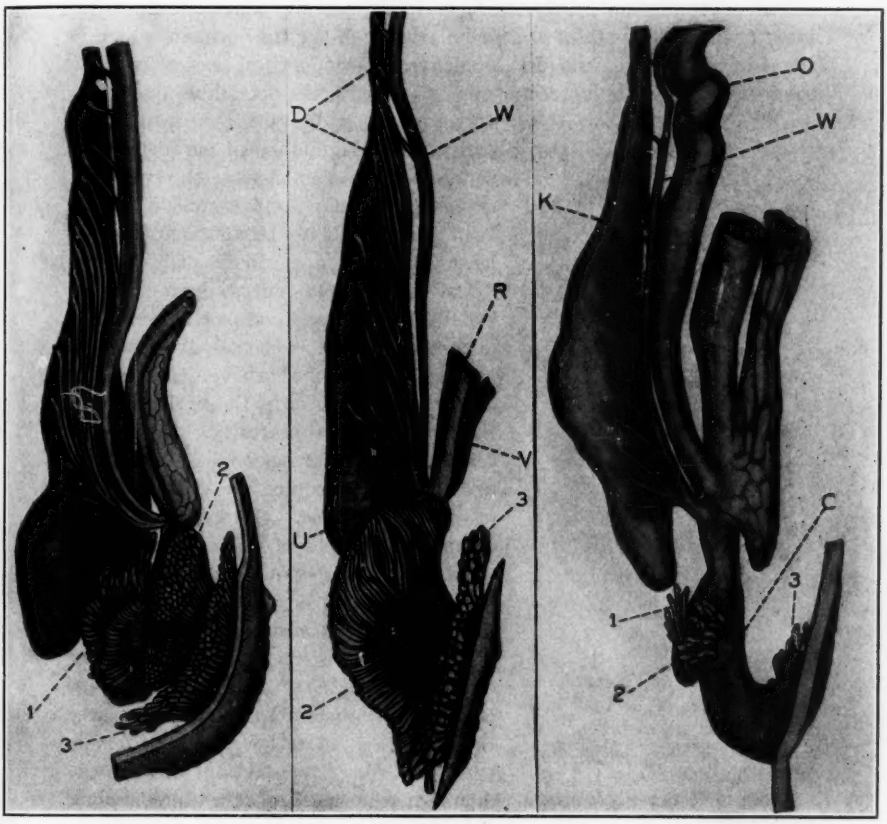


FIGURE 3 FIGURE 4 FIGURE 5

Urogenital organs of the lumbar and cloacal region of three specimens of A. jeffersonianum, dwarf race of Cedar Falls, Iowa. Age, over one year. ×10. C, cloaca; D, collecting ducts; K, lumbar kidney (metanephros); O, oviduct; R, rectum; U, ureter (metanephric duct); V, vesica; W, wolffian (mesonephric) duct; 1, 2, 3, pelvic, abdominal and labial glands.

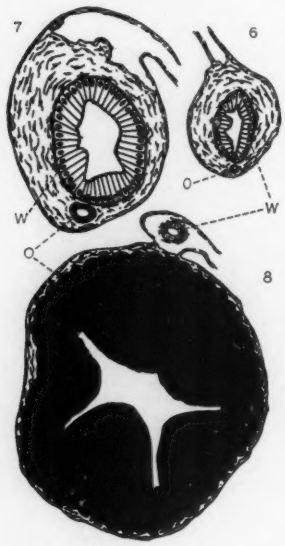
Figure 3. Sterile female (free-martin, in parabiosis with mature male of A. tigrinum).

Figure 4. Male, near maturity.

Figure 5. Female type at maturity.

inhibits ovarial differentiation of the cortex, spreads more easily and is carried by the blood stream, like a typical hormone.

The next question which had to be investigated is that of the possible identity of one or both of the medullarins with the sex hormone which in the adult stimulates the development of secondary sex characters. In salamanders the sex hormones appear in distinctly detectable quantities only toward the approach of sexual maturity. By the method of parabiosis, one can beautifully demonstrate the transmission of the male sex hormone from one twin into the other. In combinations of a large Ambystoma tigrinum male with a dwarf Ambystoma jeffersonianum female the latter becomes completely sterilized during the period of larval development, as we have described above. At the age of seven to ten months the tigrinum male reaches full sexual maturity. Due to the release of testicular hormone its secondary sex characters acquire the characteristics of the adult male. However, the same course of development is also taken by the sterile female parabiont. Figure 3 shows how, by a strong development of the vas deferens, by the formation of a separate ureter and through exuberant growth of cloacal glands (1–3), the urogenital organs of these free-martin salamanders assume the male (Fig. 4) rather than the female type (Fig. 5). Cross-sections through the ducts at the level of the mesonephric kidneys prove also that development in the free-martin (Fig. 6) follows the same pattern as in the male twin (Fig. 7) rather than the female type (Fig. 8). The wolffian duct enlarges. The cells of its epithelium become high and glandular, and the surrounding connective tissue swells and assumes the spongy type characteristic for the mature male. At the same time the oviduct remains rudimentary. It is included in the distal part of the peritoneal fold surrounding the wolffian duct and is not separately visible in gross dissections (Fig. 3).



Figures 6–8. Cross-sections through urogenital ducts of salamanders at the level of the gonads. ×55. O, oviduct; W, wolffian duct.

Figure 6. Same free-martin as in figure 3.

Figure 7. A. tigrinum male, co-twin to the free-martin (Fig. 6).

Figure 8. Same female type as in figure 5.

Evidently the male sex hormone passes from one twin into the other in the same way as the inhibitive medullarin does. Nevertheless they are

different substances as is indicated by the fact that the latter inhibits ovarial development but is without direct influence on secondary sex characters, while the former does not interfere with ovarial development (Witschi[5]) but stimulates functional growth of male secondary sex characters. The medullarin is in control of a phase of the embryonic differentiation of the sex gland while the testicular hormone stimulates merely the last functional development of male secondary sex characters. The comparison of these two hormones and their reactions in parabiotic twins is of particular interest since they represent so clearly the opposed types of inhibitive and stimulative induction.

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